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On the biology of the cestode Eubothrium crassum
(Bloch, 1779)

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In the development of some helminths of Far Eastern anadromous salmonid fishes, cases deviating from the usual type of their development are observed. Among such helminths belong the cestode Phyllobothrium caudatum (Zschokke and Heitz, 1914) and the acanthocephalan Bolbosoma coenoforme Heitz, 1920. The plerocercoid stage of the cestode Ph. caudatum is found in large numbers, sometimes in several thousands of specimens, in the intestine of Far Eastern Oncorhynchus. Adult stages of this form, as yet, are unknown. Taking into consideration the large size of representatives of the genus Oncorhynchus, it is necessary to suppose that the definitive hosts of Ph. caudatum must be pinnipeds.

Lyaiman (1937) considered that the Ph. caudatum in Amur pink salmon are more mature stages of the plerocercoid known under the name of Scolex polymorphus Rudolphi, 1819, parasitic in the gall bladder of Far Eastern fish of the genus Oncorhynchus. In a number of species of higher bony fishes, S. polymorphus is parasitic in the intestine but not developed to the stage designated as Ph. caudatum. In the intestine of the same anadromous salmon, S. polymorphus reaches a large size and changes into Ph. caudatum. However, the hypothesis of Lyaiman (1937) disagrees with the results of the experiments of Monticelli (1888) and Curtis (1911) on the ingestion of S. polymorphus by some predator fishes. These experiments indicate that plerocercoids of different cestode species, which morphologically are not distinguishable from one another, have been united under the name S. polymorphus. Divergence in the biological cycle of Ph. caudatum from the usual scheme of development consists of the fact that the plerocercoid parasite does not live in tissue, as is the location for cestodes, but in the lumen of the intestine. There are differences also in morphological characteristics of the plerocercoid Ph. caudatum, consisting of the fact that in it are the beginnings of strobilization. As correctly noted by Lyaiman (1937), Ph. caudatum is no longer a plerocercoid, but also it is not a mature cestode. It is an intermediate stage between them.

The acanthella of the acanthocephalan Bolbosoma coenoforme Heitz, 1920, is a common parasite of the intestinal tract of the majority of species of the family Salmonidae in the Far East. The sexually mature form of it is as yet unknown. Mamaev et al. (1959) expressed the supposition that it may be B. nipponicum Yamaguti, 1939, from Far Eastern pinnipeds. This acanthella, like Ph. caudatum, is parasitic in the intestinal lumen and not in tissue or in the body cavity, as is usual with the acanthella of other Acanthocephala. In morphological respects it also occupies an intermediate position between the acanthella and the adult stage. Both species - Ph. caudatum and B. coenoforme - are marine forms. We cite still another case of unusual anomaly in the development of a fish parasite. Such phenomenon [p. 6] we observed in the cestode Eubothrium crassum (Bloch, 1779). In the Far East mature forms of this cestode are found in the pyloric caeca of pink and chum salmon (Fig. 1a). Their number sometimes exceeds 1,000. In the lumen of the esophagus (near the stomach) of chum salmon are found large - up to 3.4 mm. in length and 0.45 mm. in width - plerocercoids (Fig. 1, b, c), with well defined scolex and bothria and the beginnings of strobilization. Higher in the esophagus (towards the pharynx), in the mucus, and in the walls of the esophagus in the region of the pharynx, smaller plerocercoids (1.0 - 1.2 x 0.3 - 0.38 mm.), with formed scolex and bothridia (Fig. 1, d, e), are found in cysts. Finally, the same small plerocercoids (Fig. 1, f, g, h, i), 0.5 - 0.9 x 0.29 - 0.32 mm., without a formed scolex

and only as yet rudimentary bothria are found in small (1 - 2 mm. in diameter) cysts. These cysts form a small nodular zone on the walls of the esophagus; at the place where it turns into the pharynx. As can be seen from the figures, all these parasites represent a series of transitional forms from the plerocercoid to the adult, which undoubtedly make them stages of one species. In this case attention is drawn to the [p. 7] occurrence in one and the same fish of the plerocercoid in cysts and out of cysts in the intestine, with simultaneous occurrence of mature forms. This circumstance arises from a deviation from the scheme of development of cestodes, because the lumen of the intestine or esophagus is not a usual place for plerocercoid cestodes. It should be noted that an analagous phenomenon is observed in the cestode Triaenophorus nodulosus. The plerocercoid of this species occurs in cysts in the body cavity of many species of fishes, among them also the pike. The sexually mature stage occurs in the intestine of pike. The occurrence in pike of the plerocercoid and of the mature form of Triaenophorus is readily explained by the fact that pike eat small whitefish, perch, pike-perch and other fishes and small pike infected with plerocercoids of Triaenophorus, thus becoming enriched with this helminth due to the development to the mature form of the ingested plerocercoids, and at the same time they retain in the body cavity plerocercoids acquired through feeding at an early age on crustaceans infected with plerocercoids. The example with Triaenophorus serves only as an analogy, but does not explain the case with E. crassum in chum salmon, though to some extent these cases are similar to one another. The difference between them is that in chum salmon the plerocercoids occur also in cysts in the wall of the esophagus and outside cysts in the lumen of the esophagus and intestine as intermediate forms between the plerocercoid and more mature stage, which is not observed in Triaenophorus.

There arises the question of how to treat the case of the development of plerocercoids of Eubothrium crassum in chum salmon. E. crassum is specific for fishes of the family Salmonidae and, as correctly noted by Polyanskiĭ (1955) and Mamaev et al. (1959), it is an estuarine-freshwater form. It has been found in resident dolly varden char, Salvelinus malma curilus, which have never entered the sea, and in downstream migrant young sockeye and dolly varden char, not yet having been either in estuaries or in the sea; on the other hand, it occurs in chum and pink salmon migrating from the sea to spawn. In this case mature forms are also found, having developed from plerocercoids with which fish are probably infected during the downstream migrant stage. Together with them [adults] in chum salmon, plerocercoids are also found, with which fish are infected, as Mamaev et al. (1959) supposed, during anadromous migration in estuaries. The presence of large, mature forms of E. crassum in the intestine of chum salmon migrating from the sea to spawn is fully explained by the fact that during two to three years residence in fish in the sea E. crassum grows and develops, although Mamaev et al. (1959) considered that E. crassum does not develop in the marine period of the life of the salmon; with that we cannot agree. As a matter of fact, can the cestode strobila exist in the intestine of the host, i.e., in naturally optimum conditions, for a long period without development? It is hardly possible to admit to the idea that E. crassum reaches sexual maturity during the period of catadromous migration of its host somewhere in the estuary, while not producing eggs during the two to three years residence of chum salmon in the sea. We believe that in the marine period of its life in the salmon E. crassum develops and produces sexual products, which is verified by the finding of mature specimens of E. crassum by Mamaev et al. in the

Pacific Ocean. Since E. crassum discharges enormous numbers of eggs in the sea, it is necessary to assume that in the process of evolution these eggs were swallowed by some host, as yet unknown to science, in which they were able to develop. Probably this is some crustacean, serving as a food item for salmon during the period of their feeding migration. In the period of catadromous migration the downstream migrant young are infected with E. crassum in fresh water, by feeding on freshwater crustaceans. Thus, from the literature (Rosen, 1919; Sheer [sic], 1951) it is known that in Europe small cyclopid copepods (Cyclops strenuus, Eucyclops serratulus) serve as the first intermediate hosts for E. crassum, the plerocercoid occurs in Perca fluviatilis [p. 8] and salmonid fishes serve as the final hosts, in the intestine of which the plerocercoid matures to the adult.

If we accept the assumption of the existence in the sea of some first intermediate hosts of E. crassum, then also the fact of the presence of encysted plerocercoids in the walls of the esophagus of chum salmon becomes understandable. However, the simultaneous presence of the plerocercoids in the walls of the esophagus and in the lumen of the esophagus and intestine, and also the occurrence of mature specimens in the intestines of chum salmon migrating to spawn, upsets our idea of the usual life cycle of E. Crassum and requires an explanation. If we consider the idea that the plerocercoid of E. crassum, found in the walls of the esophagus of chum salmon, establishes there during the time of its downstream migrant stage and exists there during the course of three summers, then how is it possible to explain their escape from the cyst into the lumen of the esophagus and development to maturity? But usually cestodes such as this are not known. Plerocercoids which get into chum salmon transform into plerocercoids, encyst, develop and escape from cysts, reaching maturity in the lumen of the intestine of chum salmon. Thus, as we see it, E. crassum, in association with the transition of salmon to the anadromous way of life, developed parallel to the freshwater cycle, an abbreviated or combined cycle, adapted to marine conditions, in which the second intermediate and final hosts are combined in one fish. If it is taken into consideration that the genus Oncorhynchus (as also its parasite E. crassum) is of freshwater origin and only recently changed to an anadromous way of life, which forced its parasites to adapt to new conditions also, the hypothesis expressed by us becomes more probable. Undoubtedly, the departure of E. crassum from the usual developmental cycle, as noted by us, is associated with the change of salmon to an anadromous way of life.

Mamaev et al. (1959) considered the aberration in the development of Ph. caudatum and B. coenoforme as the result of the loss of the freshwater parasite fauna with the change of salmonid fish to an anadromous way of life, while their marine parasite fauna still has not had time to build up.

The example of E. crassum cited by us enlarges the range of helminths with an unusual life cycle which occur in anadromous salmonid fishes in the Far East. The example under consideration indicates the ability of helminths to change set life cycles in the process of adaptation to a new habitat.

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¹[Translator's note. A. Kh. Akhmerov cited the title of this paper incorrectly. "Dalnevostochnykh" (Far Eastern) should have read "severnnykh" (northern).]

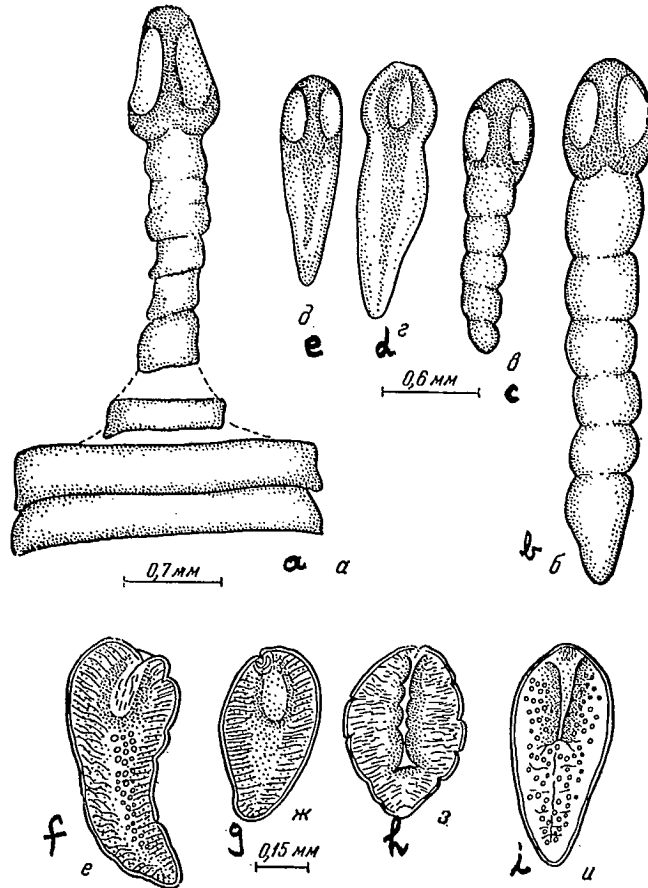


Fig. 1. Eubothrium crassum

a - mature worm, schematic; b, c - plerocercoids from the esophagus and intestine; d, e - same from cysts and mucous in the esophagus; f, g, h, i - same from cysts on the esophagus.